

1

2 **Patterns in departure phenology and mass gain on African non-breeding territories**
3 **prior to the Sahara crossing for a long-distance migrant**

4

5 Alice Risely^{1*}, Emma Blackburn² & Will Cresswell²

6 ¹Centre of Integrative Ecology, Deakin University, Geelong, VIC 3220, Australia

7 ²Centre for Biological Diversity, University of St Andrews, Harold Mitchell Building, St Andrews, Fife
8 KY16 9TH, UK & AP Leventis Ornithological Research Institute, Jos, Nigeria

9

10 * Correspondence author: riselya@gmail.com

11

12

13 **Keywords:** migration, Palaearctic migrant, phenology, stopover, departure, fuel deposition

14

15 Abstract

16 Afro-Palaeartic migrants are declining to a greater degree than other European species, suggesting
17 that processes occurring in Africa or on migration may be driving these trends. Constraints in food
18 availability on the wintering grounds may contribute to the declines but little is known about when
19 and where these resource constraints may occur. Sufficient resources are particularly important prior
20 to spring migration, when migrants must cross the Sahara desert. We examined mass gain and
21 departure phenology in a long-distance Palaeartic passerine migrant to determine the degree to
22 which pre-migratory fattening occurs in their long-term non-breeding territories in the Guinea
23 Savannah region of Africa. We monitored 75 Whinchats *Saxicola rubetra* for departure from their non-
24 breeding territories in one spring, and analysed mass data of 377 Whinchats collected over three non-
25 breeding seasons plus 141 migrating Whinchats caught in April over eight years, all within the same
26 few square kilometres of anthropogenically-modified Guinea Savannah in central Nigeria. Whinchats
27 left their winter territories throughout April, with males departing on average eight days earlier than
28 females. However, there was no evidence that time of departure from territory was linked to age,
29 body size or mass at capture. Whinchats departed their territories with a predicted mass of 16.8 ± 0.3
30 g, which is much less than the ~24 g required for the average Whinchat to cross the Sahara directly.
31 Comparing departure dates with arrival dates in southern Europe shows a discrepancy of at least two
32 weeks, suggesting that many Whinchats spend considerable time on pre-migratory fuelling outside of
33 their territory prior to crossing the Sahara. Over-wintering birds gained mass slowly during February
34 and March (0.03 g d^{-1}), and non-territorial or migrating birds at a much higher rate in April (at least
35 0.23 g d^{-1}), with up to 20% of migrating Whinchats in April potentially having sufficient fuel loads to
36 cross the Sahara directly from central Nigeria. Our results suggest that most Whinchats leave their
37 winter territories to fatten up locally or, possibly, by staging further north. Resource constraints are
38 therefore likely to be particularly focussed in West Africa during mid-April and possibly at staging areas
39 before the crossing of the Sahara desert.

40 Introduction

41 Pronounced declines of long-distance Afro-Palaeartic migrants in comparison to other European
42 species point towards mechanisms operating on African wintering grounds as possible drivers
43 (Bohning-Gaese & Bauer 1996, Sanderson *et al.* 2006, Heldbjerg & Fox 2008). Limited resources on
44 the wintering grounds, especially prior to spring migration, may contribute to these declines (Baillie
45 *et al.* 2008) by constraining spring fattening and delaying spring departure (Marra *et al.* 1998, Studds
46 & Marra 2005, 2011). Additionally, migrants wintering in the Sahel region face one of the largest
47 barriers in the world, the Sahara desert, and therefore availability of adequate resources to sustain a
48 >2000 km flight during early spring is of critical importance.

49 There is some evidence, however, that food resources around the semi-arid Sahel or Guinea Savannah
50 wintering grounds may not be a limiting factor for more generalist migrant species, which many long-
51 distant migrants are thought to be (Cresswell 2014; see Ockendon *et al.* 2012 for species classifications
52 and trends). For example, Ockenden *et al.* (2012) showed that generalist species are generally
53 increasing in comparison to specialists, even those wintering in the African humid and southern
54 bioclimatic regions associated with strong migrant population declines. Furthermore, Hulme &
55 Cresswell (2012) found that typical human-modified habitat in the Guinea Savannah zone of West
56 Africa may not limit Whinchat density, and this indicates that, where suitable habitat is present and
57 species are not at carrying capacity, individuals may be fully capable of not only surviving but also
58 fattening up in preparation for spring migration in these habitats. This is supported by the fact that
59 energy requirements in the tropics and sub-tropics are relatively low (Wikelski *et al.* 2003); for
60 example, wintering Whinchats spend only 11% of their time foraging (Barshep *et al.* 2012), and the
61 process of meeting energy budgets outwith of migration in sub-tropical savannahs may only require a
62 few hours foraging a day (Brandt & Cresswell 2009). If this is the case, then overwintering migrants in
63 the Sahel and Guinea Savannah regions may be able to gain sufficient mass for the first major leg of
64 their spring migration - the crossing of the Sahara - without leaving their territory or home range. This
65 strategy would have the advantage of minimizing the risk involved in searching for food in potentially

66 unknown areas (Cresswell 2014), plus reduce the number of staging locations, a factor hypothesised
67 to be relatively important during spring migration when time schedules are tighter than in autumn
68 (Hedenström & Alerstam 1997, Weber & Houston 1997; but see McKinnon *et al.* 2013).

69 This study aimed to explore spring departure phenology from African wintering territories in a long-
70 distance migrant, the Whinchat *Saxicola rubetra*, and link this to patterns in mass gain over the
71 wintering period in order to infer to what extent pre-migratory fattening occurs on territory. We also
72 compared departure dates from territory to phenology data from stopover sites in southern Europe
73 to further determine whether there was time available between departure and arrival in Europe for
74 additional pre-migratory fuelling.

75 The Whinchat is an Afro-Palaeartic migrant that breeds from western Europe east to Siberia, and
76 winters in eastern central Africa and south of the Sahel in open landscapes and farmland (Cramp
77 1988). Although widespread, Whinchats have undergone significant declines over much of their range
78 over the last 20 years (BirdLife International 2004, Henderson *et al.* 2004). This is thought particularly
79 to be due to changes in land use on their European breeding grounds affecting breeding success rather
80 than their wintering grounds (Müller *et al.* 2005; Gruebler *et al.* 2008); nevertheless, ecological
81 interactions on the non-breeding grounds will be important for any migratory species. Individuals
82 hold small, distinct territories during the winter (Barshep *et al.* 2012, Blackburn & Cresswell 2015a),
83 and their preference for open habitat and tendency to perch on low shrubs make them highly
84 detectable (Hulme & Cresswell 2012).

85 We monitored individually marked Whinchats on a daily basis for departure from their long-term
86 territories over several neighbouring sites (within the same 40 km² location) in central Nigeria
87 (hereafter referred to as 'resident' Whinchats) to study departure patterns. We used mass data from
88 the same resident population collected over three non-breeding seasons, combined with mass data
89 from migrating individuals of unknown origin, but caught in an area within the same location but

90 where Whinchats do not hold territories (i.e. 'non-resident') in April, to analyse temporal patterns in
91 mass gain on and off territory within the same location prior to the crossing of the Sahara.

92 If birds depart on migration straight from their wintering territories then a series of predictions
93 regarding departure timing and mass can be made:

94 1) Departure timing from territory for the population should match arrival times in southern Europe
95 (arrival times on the Italian island of Capri: late-April – mid-May; Jonzen *et al.* 2006) with an estimated
96 lag time of around a week to cross the Sahara (a conservative estimate based on birds crossing 2500
97 km at 36 km/hour for 12 hours per day = 5.8 days; Pilastro & Spina 1997, Schmaljohann *et al.* 2007,
98 Delingat *et al.* 2008). We focus on southern Europe rather than eventual breeding grounds as these
99 areas represent likely first refuelling stopover sites after the Sahara crossing.

100 2) Individuals will depart when they reach a mass that allows them to cross the Sahara. The Sahara
101 border is 400 km north of the study site (an 11 hour flight for a small passerine), and the crossing from
102 central Nigeria is a minimum journey of 2500 km, which is calculated to require 100% fuel load for a
103 Whinchat (see Delingat *et al.* 2008). This is equivalent to a mass of approximately 24 g. Alternatively,
104 if masses on departure are lower than these levels this would suggest that Whinchats add mass
105 outside of their winter territories. If subsequent fattening can occur in the same area (i.e. within a few
106 kilometres of the territory) then we would expect that Whinchats caught outside of their territories
107 but still in the local area to show levels of mass that will allow them to cross the Sahara.

108 3) Birds may depart with a mass dependent on their dominance status (age) because territory quality
109 is likely to correlate with dominance status (Piper 1997). Sub-dominant birds in their first winter
110 (controlling for sex because males may inherently leave earlier than females to re-establish breeding
111 territories; Maggini & Bairlein 2012) may depart later or with lower mass than birds of greater age and
112 experience because they occupy lower quality territories.

113

114 Methods

115 *Study system*

116 The study took place over three non-breeding seasons (September - April) between 2012 and 2014 on
117 the Jos Plateau in the Guinea Savannah zone of Nigeria, West Africa (09°53'N, 08°59'E) where many
118 Afro-Palaeartic migrants winter (Fig. 1). We studied six sites over a 4000 ha area east of Jos
119 containing typical overwintering habitat for Whinchats. Sites consisted of degraded Guinea Savannah:
120 open scrub with moderate levels of grazing and small subsistence farming. Sites were selected on the
121 basis of containing suitable Whinchat habitat and for logistical reasons, and did not differ significantly
122 in habitat characteristics (Blackburn & Cresswell 2015a). Sites ranged from 50 to 200 ha in size, were
123 no more than 2 km apart, and were surrounded by similar areas of habitat. Whinchats were common
124 at a much larger scale around the whole study location (see Hulme & Cresswell 2012).

125 Whinchats were caught with spring traps with live bait and mist nets, both using a playback lure. All
126 captured birds were uniquely colour-ringed. Most individuals were either captured in the winter of
127 2014 or had returned to territories occupied in previous winters, resulting in a population of
128 individually recognisable resident birds for departure study in April 2014. We fitted geolocator devices
129 (~0.65 g; see Appendix A for permit information) to approximately half of the birds as part of a tracking
130 study not considered here, but the opportunity was used to examine the effects of experimental
131 application of additional mass on departure dates. Data from non-resident Whinchats of unknown
132 origin (either migrants passing through or local birds off their territories) were collected as part of a
133 Constant Effort Ringing Scheme (CES; see Stevens *et al.* 2013 for details) during April from 2002 to
134 2013 inclusive, in an area adjacent to the territorial study areas where few whinchats hold territories
135 (Fig. 1).

136 Flattened wing chord length (to the nearest 0.5 mm), tarsus length (to 0.1 mm), body mass (to 0.1 g
137 using digital scales) and moult score were measured following Svensson (1992). Whinchats were sexed
138 and aged as either first-winter (hatched the previous year; EURING code 5) or adult (hatched before

139 the previous year; EURING code 6), using a combination of features described by Svensson (1992) and
140 Jenni & Winkler (1994). Detailed photographs were taken of all birds, and age and sex were
141 independently corroborated by both A.R. and E.B.

142 ***Estimating departure dates***

143 Mapping of marked individuals was carried out at all six sites from 3rd March 2014 by systematically
144 walking each site every two to four days using binoculars and a telescope. Whinchats characteristically
145 spend 80% of their time perching on the top of small bushes in open habitat (Barshep *et al.* 2012),
146 therefore we could accurately identify the majority of individuals present during any visit. From 2nd
147 April, known territories of marked birds at three of the six sites (for purposes of practicality) were
148 visited almost daily to monitor for departure (mean number of visits over 24 days per individual = 20.1
149 \pm 3.4 SE, n = 1509 total visits; including a decrease in territory visit frequency once an individual was
150 not seen for five consecutive visits). If an individual was not resighted after five consecutive visits then
151 it was assumed departed from its winter territory. All territories were visited at least every two-three
152 days over the entire monitoring period to confirm absence and detect whether individuals were
153 moving over a larger local scale than their winter territory just prior to departure. Territorial birds are
154 extremely site-faithful: only one bird was recorded moving ~500 m from original territory prior to
155 departure after unusual weather conditions and no others were seen outside their territories during
156 departure monitoring.

157 Departure was measured as relative days after the first bird departed (day zero; 1st April). Only
158 individuals which were consistently seen on territory (i.e. resident in the study area over winter) were
159 included in analyses (n = 75). Birds visited four times or less during April before they departed were
160 only included if they had been resighted regularly on territory prior to daily departure monitoring
161 beginning (n = 5). These birds departed between 25th March and 1st April and were assigned a
162 departure date of day zero (1st April) because their exact departure date was unknown. Although error
163 in departure is higher for these individuals than the rest, excluding them from analyses did not

164 significantly change any results, therefore they were retained in analyses. Additionally, assuming these
165 five birds departed the day after they were last resighted as opposed to 1st April did not significantly
166 affect mean or standard deviation of departure date across the monitored population (13.0 ± 8.1 SD
167 and 13.4 ± 7.25 SD days after 1st April respectively). Error in departure was calculated to be 1.4 ± 1.1
168 SE days after last resighting ($n = 70$; Appendix B).

169 ***Analysis***

170 *Modelling departure*

171 Model selection for all analyses was carried out using the information-theoretic approach based on
172 Akaike's Information Criterion (AIC; Burnham & Anderson 2002). Candidate general linear models
173 (LM) were first constructed using the subset of the birds captured in 2014 which had biometric and
174 mass data collected within 3 months of departure ($n = 57$). Age, sex, wing length, tarsus length, mass
175 and time of day were included as main effects. Site and attachment of geolocator were also included
176 as fixed factors to control for any confounding effect they may have had. Replacing tarsus and wing
177 length with a single principal component that summarised 53% of the variation did not change any of
178 the models in terms of biological or statistical significance. Component models were compared using
179 AIC, and where there was no clear optimum model, model averaging was applied (including candidate
180 models with $\Delta AIC < 4$) and variable estimates and importance are presented. Because we lacked
181 recent body size data for 18 individuals, candidate models were constructed again for all birds but
182 excluding mass, wing and tarsus lengths to maximise sample sizes, and model selection repeated as
183 above. Where individuals had been captured multiple times in 2014, we used the most recent capture
184 event data to avoid pseudo-replication and to apply the mass nearest to departure. Using first
185 captures instead makes no difference to model selection outcome. Repeating analyses with all
186 captures and recaptures, and including individual and site as random effects in a linear mixed model
187 (LMM; lme4 package, Bates *et al.* 2014), did not affect statistical or biological results, therefore we
188 presented the simpler fixed effect models. There were no significant quadratic effects in any model.

189 *Predicting mass at departure*

190 In order to predict mass at departure, we modelled mass at capture against days until departure (from
191 capture) using a general linear model for all resident birds sampled, controlling for tarsus length, age,
192 sex and time by including these as predictor effects and comparing candidate models using AIC. The
193 best model included only mass (days until departure \sim mass; see results), indicating that mass at
194 capture is related to when the individual will depart from that date. Because the intercept of the
195 model (mass at 0 days = departure) is an extrapolation as we lacked samples from birds less than 6
196 days before departure, fitting a linear relationship including any time prior to the commencement of
197 mass gain would bias our estimate of departure mass downwards. Therefore we carried out a
198 sensitivity analysis (reported in the results), reducing the sampling period to samples less than 70 days
199 from departure, then to samples less than 60 days from departure, and so on, to ascertain any change
200 in rate of mass gain prior to departure.

201 *Mass patterns over non-breeding season*

202 Patterns in mass gain were analysed using birds with complete biometric data captured over the three
203 non-breeding seasons of the study to increase sample sizes and to allow description of mass over the
204 entire winter period as well as departure ($n = 377$). Where birds were caught more than once, the
205 first capture event data was used, unless any data was missing for first capture or there was a capture
206 available in March or early-April, when this single capture was used instead to balance sample sizes,
207 because there were many fewer captures during March and April during the study.

208 We split the wintering season into two periods (before and after 1st January) to explore strategies of
209 mass gain over the winter: a model containing all data showed a significant interaction between these
210 two periods and mass gain trajectory so justifying this split (see results). Candidate models predicting
211 mass were constructed using sex, age, tarsus, wing, date, time, season, site and stage of pre-breeding
212 partial moult (moulting/not-moulting as a 2-way factor) as main effects, and compared using AIC as
213 above.

214 We estimated mass gain for non-resident Whinchats using the CES April mass data. An LM model was
215 constructed with mass as dependent variable and date, sex, time, wing, year and site as predictors,
216 using as similar models as possible to that found for the resident birds in the second half of winter
217 (described above and in the results below) so that mass patterns would be as comparable as possible.
218 As most birds had finished moulting by April we did not include moult stage. We compared predicted
219 mass gain between the two models (i.e. February and March period against April) by comparing the
220 confidence intervals of the parameter estimates for date. We did not model all the data together
221 because they were collected at different sites, and the CES data was missing a reliable estimate of age
222 and tarsus for most individuals. We used these CES data only to test whether fuelling rates
223 (acknowledging that any estimate will be an underestimate; Minias & Kaczmarek 2013) were different
224 for birds that were not on winter territories or on passage.

225 *Calculating flight ranges*

226 Flight ranges were calculated in the following way: to calculate the average fuel load (f), the following
227 equation was used: $f = [(m - m_i) / m_i]$, where m = actual mass and m_i = lean body mass (LBM) (Delingat
228 *et al.* 2008). An average lean body mass of 12.8 g was used, based on the average mass of Whinchats
229 captured after crossing the Sahara with fat and muscle scores of zero (Pilastro & Spina 1997). A lower
230 average lean body mass of 11.6 g was identified by Salewski *et al.* (2010), and although using this value
231 did not alter final conclusions, we include ranges calculated from this value in the text as an example
232 of what is possible for a Whinchat if it utilizes all possible energy reserves (including muscle mass).
233 These two values were used because very few Whinchats were recorded in this study in poor condition
234 (i.e. very low fat and muscle scores); therefore we suggest they did not accurately represent lean body
235 mass. The 12.8 g value was similar to the lightest Whinchats recorded on our site, with 25% of captures
236 under 14 g. Applying parameters higher than 12.8 g resulted in very high expected departure mass,
237 which have not been recorded in sub-Saharan Africa, supporting the use of these chosen LBM
238 parameters. Flight range in km (Y) from estimated fuel load at departure was calculated using the

239 method according to Delingat *et al.* (2008): $Y = 100 \times U \times \ln(1 + f)$, where U = ground speed and f = fuel
240 load. We used the air speed of 36 km h⁻¹ reported for small passerines (Bruderer & Boldt 2008).

241 Analyses were carried out in R software version 3.1.1 (R Core Team 2014). All means are given \pm 1
242 standard error (SE) unless otherwise stated.

243 Results

244 *Phenology of departure*

245 In total, 75 individually marked Whinchats were monitored for departure over April 2014 in central
246 Nigeria. Birds departed over a four-week period between 25th March and 24th April 2014 (mean = 14th
247 April \pm 7.3 SD days; Fig. 2).

248 Sex was retained in all top models predicting departure for individuals with recent mass and biometric
249 data (captured in February and March 2014, $n = 57$), and was the only factor retained in the top model
250 (Table 1a). Model averaging of all models with $\Delta AIC < 4$ also resulted in sex being the only significant
251 factor influencing departure date (Table 2a).

252 Repeating the analysis with all birds ($n = 75$, Table 1b) confirmed that sex was still the only significant
253 factor: although site was retained in the top model, model averaging indicated that site was not a
254 significant predictor (Table 2b). The optimal model to predict departure timing therefore contained
255 sex only ($F_{1,75} = 31.5$, $R^2 = 0.30$, $p < 0.0001$), with males leaving on average 8 days before females (Fig
256 2). Departure was not significantly related to age, although statistical power for males was low due
257 to low numbers of first winter males (adults: $n = 21$; first-winter: $n = 9$). However, there was clearer
258 evidence that there was no difference in departure timing between adult and first-winter females
259 (adults: $n = 26$, first-winter: $n = 19$; Fig 2). Whether a bird had been fitted with a geolocator was
260 retained in some of the top models when all birds were included, although it was not a significant
261 factor when averaged out across top models, nor was it statistically significant in the models in which

262 it was retained. These models in any case predict a very small biological effect: birds with a geolocator
263 left on average 1.4 ± 4.3 days earlier than birds without geolocators (Table 2b).

264 ***Mass gain at departure***

265 Days until departure from time of capture significantly predicted mass with an intercept (i.e. predicted
266 mass on departure) of 16.8 ± 0.3 g, using all data from less than 80 days before departure (Fig. 3).
267 Rates of mass gain over the period sampled (6 – 77 days before departure) were 0.03 ± 0.007 g per
268 day (Fig. 3). The value of the intercept did not change significantly between periods sampled (birds
269 captured within 80 days from departure as above, $n = 57$; <70 days, intercept = 16.8 ± 0.3 g, $n = 55$;
270 <60 days, 16.5 ± 0.4 g, $n = 45$; <50 days 16.2 ± 0.4 , $n = 36$; <40 days, 16.5 ± 0.5 , $n = 25$; <30 days, 16.9
271 ± 0.6 , $n = 21$: see Fig. 3) suggesting that the intercept calculated using all of the available data was
272 robust for the period up until 6 days before departure.

273 ***Comparing phenology with southern Europe***

274 Whinchats pass through the Italian island of Capri between 22nd April (mean of earliest 10th percentile)
275 and 12th May (mean of the latest 10th percentile; Jonzen *et. al* 2006 supplementary material): note
276 that there are almost no ringing recoveries of Whinchats in Africa and so limited data to support this
277 route except for a single Whinchat ringed on the study site recovered on spring passage in Northern
278 Italy (unpublished data) and our own preliminary geolocator data which shows this route is common
279 (unpublished data). This range of 20 days is similar to the departure range in our population study,
280 and indicates that there is a three-week period between birds departing territory and arriving in
281 southern Europe.

282 ***Seasonal mass gain patterns***

283 An overall model using mass data of 377 resident colour-ringed Whinchats showed that the
284 relationship between mass and date was significantly dependent upon whether a Whinchat was
285 captured before December or after January (period * date, additional mass gained in the second

286 period with date = $0.026 + 0.01 \text{ g}$, $t = 3.7$, $P < 0.001$; full model including all variables in Table 3, overall
287 adjusted $R^2 = 0.34$, $F_{16, 360} = 13.3$, $P < 0.0001$; Fig. 4). Models predicting mass in the first half of the non-
288 breeding season show that only tarsus length, wing length and year of capture were retained in the
289 top models (Table 3a), and also had high importance when averaged out across top models (Table 4).
290 Birds caught in 2013 were slightly heavier than those caught in 2012. Sex, age, date of capture, site
291 and time of day were rarely retained in top models and model averaging across top models confirmed
292 that these variables had low importance: during early winter mass remained uniformly low (Fig. 4). In
293 contrast, model comparison for the second half of the wintering period presented a clear optimum
294 model which retained tarsus length, sex, age, date of capture, time of day, stage of moult and site as
295 predictors of mass (Table 3b; full model coefficients in Table 5). The Akaike weight of this model shows
296 that it was 2.3 times more likely than the next ranking model ($\omega = 0.57$ versus 0.25) which additionally
297 retained wing length. This model predicted that mass in the second half of the wintering season
298 increased with date, tarsus length, time of day, moult stage and that males were heavier than females
299 (Fig. 4) and adults were heavier than birds in their first winter (Table 5).

300 There were 141 captures (no recaptures) in April from the CES (constant effort ringing; 5 in 2002, 30
301 in 2003, 16 in 2004, 18 in 2007, 7 in 2008, 14 in 2010, 10 in 2011 and 41 in 2013) from non-resident
302 birds. Mass increased significantly with date in April ($0.228 \pm 0.063 \text{ g/day}$, $t_{1,127} = 3.6$, $P = 0.0005$; Fig.
303 4) controlling for year, time of day, location, wing length and sex, and the confidence limits of this rate
304 of change did not overlap with the confidence limits of the much lower rate of change during January
305 to March ($0.031 \pm 0.009 \text{ g/day}$; note the coefficient differs slightly from this value given above because
306 a slightly different model structure was used to allow the most similar comparison possible between
307 resident bird data and that from the CES transient birds, due to tarsus length and age not being
308 available for CES data). Males were also heavier than females throughout April ($1.4 \pm 0.5 \text{ g heavier}$, $t_{1,127} = 2.9$, $P = 0.008$; Fig. 4).

310 **Flight ranges**

311 A fuel load of 100% LBM was calculated to be required to cross the Sahara from the study site in
312 central Nigeria (~2500 km), and 74% LBM from the Saharan border (~2000 km). A mass of 16.8 g –
313 the predicted departure mass from territory for the resident birds in 2014 – was calculated to be
314 between 31% or 45% of lean body mass, which allows an estimated flight range of 979 km or 1333 km
315 (depending on whether the higher or lower LBM was used, respectively; Fig. 5). If we use the range of
316 observed body masses (n = 141) from April CES non-resident birds then predicted ranges vary
317 considerably. Assuming a higher lean body mass then c. 5% of Whinchats in April could cross the
318 Sahara directly from the study site at Jos without a stopover, and assuming the lower lean body mass
319 then 20% of Whinchats could directly cross the Sahara (Fig. 5).

320 Discussion

321 Whinchats departed their wintering territories in central Nigeria between late March and late April,
322 with males departing earlier than females on average; however, no patterns relating to age, body size
323 or condition at capture were found. Departures were unlikely to have been confounded by mortality
324 because winter survival rates for Whinchats are extremely high, with probability of return the
325 following year being unrelated to the timing of departure (Blackburn & Cresswell; unpublished data).
326 Whinchats were predicted to depart from territory with an average mass of 16.8 g, 31 - 45% of lean
327 body mass (LBM). This suggests that most Whinchats do not have sufficient fuel loads for a direct 2500
328 km minimum crossing of the Sahara (i.e. without further fattening) when they leave their primary
329 winter territories, a journey which is calculated to require 100% LBM (23.2 – 25.6 g) from central
330 Nigeria. Moreover, it suggests that Whinchats at most only start to fatten up on their winter
331 territories, and then depart with relatively low fuel reserves to fatten up elsewhere, possibly further
332 north. The small and gradual amount of mass gain from January to March is perhaps more consistent
333 with physiological changes, including increased reserves to deal with the cost of moulting (see Lind &
334 Gustin 2004, Bauchinger & Biebach 2006, Fox & King 2013) and increased fat reserves associated with
335 increasing foraging unpredictability as the dry season progresses (McNamara & Houston 1990,

336 Houston & McNamara 1993). Although it is possible that many individuals could potentially have
337 gained more mass on territory between capture and departure from their territory, it is very unlikely
338 that the individuals captured within two weeks of departure ($n = 8$) had enough time to gain enough
339 mass on territory, and probably impossible for those caught within a week of departure ($n = 4$).
340 Maximum fuel deposition rates found in comparably sized species Common Redstart *Phoenicurus*
341 *phoenicurus* and Common Whitethroat *Sylvia communis* on stopover in Senegal during spring
342 migration were found to be between 2.6 ± 2.2 and $3.5 \pm 2.6\%$ LBM/day, respectively (Bayly *et al.* 2012;
343 no information on the Whinchat available), which translates to a mass gain of 0.3 - 0.5 g per day for
344 the average Whinchat. It is therefore unlikely that many of the sampled resident Whinchats, even if
345 they were indeed fattening up at a faster rate just prior to departure from their territory, would be
346 fuelling at a sufficient rate to reach a mass sufficient to cross the Sahara.

347 Comparing departure dates from territory to arrival timing in southern Europe also provides evidence
348 that pre-migratory fattening occurs after departure from territory. Whinchats pass through the Italian
349 island of Capri (likely to be one of the first stops for many migrants after the Sahara) three weeks after
350 departing territories in Nigeria. This period is much longer than expected if birds were leaving directly
351 from their wintering territories if it takes only 2 – 6 days to cross the Sahara (Schmaljohann *et al.* 2007,
352 Delingat *et al.* 2008). Our unpublished geolocator data shows that Whinchats cross the Sahara directly
353 without stopping and then refuel in North Africa for several days (Blackburn *et al.* unpublished data).

354 There are three non-mutually exclusive possible explanations for why birds may not reach maximum
355 fuel load on winter territory: 1) limited resources on a small territory do not allow sufficient fuel
356 loading to cross the Sahara, and therefore birds abandon their territory to search for better quality
357 habitat locally; 2) habitat quality in the area is not sufficient for migratory fuelling and therefore birds
358 abandon their territory and move out of the local area to find better quality habitat regionally; or 3)
359 resources on territory or locally are not limiting but birds move north as a strategy to reach maximum
360 fuel loads closer to the Sahara desert, the border of which begins roughly 400-500 km further north,

361 even though fattening on territory (and/or locally) is possible. Our results suggest that habitat quality
362 in the area generally is not a limiting factor, with 5 - 20% of transient individuals caught locally
363 potentially able to cross the Sahara at the time of capture, although it cannot be ruled out that these
364 birds fattened up further south. However, there was little evidence that birds were staying in the local
365 area encompassed by the study sites to fatten up because no colour-ringed birds were resighted
366 between sites in April or were caught nearby at the CES site over the three-year study period.
367 Therefore the most likely explanation may be that birds are moving further north to fatten up as close
368 to the desert barrier as possible. Although individuals with sufficient fuel loads to cross the Sahara
369 are captured in the region, the average mass in April is around 20.0 ± 3.3 g (see also Smith 1966 which
370 reports almost identical masses at a nearby site in central Nigeria), indicating that most Whinchats
371 reach some level of migratory condition in this region, but may delay depositing the maximum fuel
372 load until further north. Although very few data exist for Whinchats in northern Nigeria, Fry (1969)
373 found slightly lower masses (19.2 g [SD not reported], $n = 11$), which would be consistent with birds
374 requiring lower fuel loads to cross a shorter distance, although more data is needed to confirm this.
375 Agriculture and vegetation extends another 400 km north to the edge of the desert from Jos, and
376 important wetlands such as Hdejia-Nguru and Lake Chad lie 350 and 600 km to the northeast
377 respectively. Although Whinchats are unlikely to be found in typical wetland habitat in the non-
378 breeding season (e.g. Bayly *et al.* 2012), the surrounding vegetation and farmland may provide crucial
379 resources in gaining sufficient fat for the >2000 km desert crossing from the desert border.

380 The hypothesis of moving north to fatten up is consistent with other studies which have shown that
381 passerines tend to delay depositing large fuel loads during migration until reaching a major ecological
382 barrier, such as the Sahara (Schaub & Jenni 2000, Ottosson *et al.* 2005), and that timing of maximum
383 fuel loading is inherently linked to the latitude of these barriers (Fransson *et al.* 2001). Depositing
384 maximum fat loads as late as possible avoids the increased predation risk associated with high fuel
385 loads (Kullberg *et al.* 1996, Dierschke 2003) and the maintenance of high body mass (Alerstam &
386 Lindström 1990, Klaassen & Lindström 1996). Departing from 400 km further north at the desert

387 border reduces the required fuel load to cross the Sahara by at least 25%, which may outweigh the
388 advantages of remaining on territory or in central Nigeria. However, Ottosson *et al.* (2005) found
389 evidence that many Garden Warblers (*Sylvia borin*) had sufficient mass to depart directly from this
390 zone in the spring, rather than moving north, suggesting that other species may have different
391 strategies, or their “barrier” starts at a lower latitude or that the best fattening area is in the Guinea
392 Savannah. An alternative hypothesis, of course, is that migrants can refuel during stopovers in the
393 Sahara: whether this is strategy at all for Whinchats requires further study.

394 Although we cannot measure mass gain immediately prior to departure, if mass at departure was an
395 important driver of departure then patterns in mass gain over the non-breeding period may indirectly
396 affect departure timing, for example, via processes such as dominance-based habitat segregation
397 whereby dominant birds (e.g. males and adults) have access to the best resources (Marra & Holmes
398 2001, Arizaga & Bairlein 2011). However, although mass in the latter part of the non-breeding season
399 differs between sexes, ages and sites – potentially indicating dominance-based access to resources –
400 this is not reflected in departure patterns, suggesting that mass is not a key driver of departure from
401 territory. Sex was the strongest predictor of departure, with males departing territories on average
402 eight days before females, reflecting patterns observed on arrival at the breeding grounds in
403 Whinchats (Tøttrup & Thorup 2008) and other migratory species (Francis & Cooke 1986, Cooper *et al.*
404 2009). However, neither age nor body size appeared to have any relationship with timing of
405 departure, although segregation by these traits is sometimes reported on arrival at the breeding
406 grounds (Stewart *et al.* 2002, Cooper *et al.* 2009, Risely *et al.* 2013).

407 In order to understand the mechanisms behind patterns in departure and mass, it should be noted
408 that migratory timing is controlled by both endogenous (e.g. circannual rhythm) and by exogenous
409 (e.g. resource availability) mechanisms (Gwinner 1986, Studds & Marra 2005, 2011, Maggini & Bairlein
410 2012). Resource availability and its relationship with condition has been identified as a significant
411 limiting factor during spring departure in the Neotropics, with American Redstarts *Setophaga ruticilla*

412 occupying better quality habitat reaching migratory condition and departing earlier on spring
413 migration than those occupying poorer quality habitat (Marra *et al.* 1998, Studds & Marra 2005). This
414 may not be the case in the Old World, however, where suitable wintering habitat may be more
415 abundant (see Newton 2008), and differences in quality between habitats are not so well defined
416 (Cresswell 2014). Indeed, there is no evidence of sex or age based habitat occupancy for wintering
417 Whinchats over the study area based on fine-scale habitat characteristics (Blackburn & Cresswell
418 2015a, 2015b), although it is possible these habitat characteristics do not necessarily reflect prey
419 abundance. A lack of segregation would be expected in an area with low competition (Whinchats are
420 not at carrying capacity in this area; Hulme & Cresswell 2012) and where energy costs are low
421 (Whinchats spend only 11% of the day foraging; Barshep *et al.* 2012), indicating that differences in
422 territory quality are probably not important for overwinter survival. In this system, patterns in
423 departure phenology may more closely reflect differences in endogenous triggers rather than
424 resource constraints. Studies on captive birds have shown that there are differences in endogenous
425 timing of migration between populations (Maggini & Bairlein 2010) and sexes (Coppack & Pulido 2009,
426 Maggini & Bairlein 2012), with males preparing for departure earlier than females independent of
427 external factors; however, this has not been shown to be linked to age, although experimental
428 evidence for this is lacking due to the difficulty is keeping individual birds captive over many years (but
429 see Sergio *et al.* 2014 for age effects in a free-living raptor species). Therefore the pattern of departure
430 we observed could be expected if departure timing from territory was triggered by endogenous
431 mechanisms and relatively unconstrained by resource limitations. If Whinchats mostly fatten up
432 outside of their territories, then territory quality cannot be a constraining factor, and therefore
433 unlikely to have a strong effect on departure timing. Resource availability and dominance-related
434 differences in access to resources may, however, become a constraining factor during migration,
435 especially prior to the Sahara crossing when individuals need to deposit larger reserves of fat to fuel
436 the desert crossing (Biebach 1992).

437 Overall, this study suggests that although this population of Whinchats may reach some level of
438 migratory condition on territory (particularly if fuel deposition rate increased a few days just before
439 territory departure), it seems more likely that most do not fatten up within their wintering territories.
440 It is unknown whether they then reach maximum mass locally or move further north to fatten up
441 closer to the Sahara, where they would require a smaller fuel load due to the shorter distance to travel.
442 Indeed, many Palaearctic migrants, including Whinchats, have been captured in April on stopover near
443 Lake Chad in north-east Nigeria (Fry 1969), although these areas have not been systematically studied.
444 This is, however, a risky strategy if resources are not limiting on territory, because it involves
445 expending energy searching for plentiful resources in unknown areas for first years on their first return
446 migration. Further research is needed to determine whether this is an inherent strategy, which might
447 in any case be expected for other wintering populations which winter further south in Kenya, Tanzania
448 and Zambia, rather than close to the Sahara border. Additionally, these calculations are based on the
449 assumption that Whinchats (and other generalist species) do not deliberately stopover in the desert
450 to feed as a strategy. Stopovers seem unlikely if migrants have sufficient resources prior to the desert
451 crossing, which many do even from local fattening as demonstrated in this study, as relying on finding
452 suitable stopover sites in the desert must be extremely risky. Additionally, Whinchats have not been
453 documented in any numbers refuelling in Saharan vegetation (Jenni-Eiermann *et al.* 2011) although
454 this is absence of evidence rather than evidence of absence.

455 In conclusion, if territorial overwintering migrants largely leave their territories to fuel up elsewhere
456 then initial winter territory selection may not be influential for Palaearctic passerine migrants because
457 low quality territories may suffice in terms of over-winter survival (Cresswell 2014). However, the
458 quality of staging sites (i.e. their potential to provide sufficient resources for large and rapid mass gain)
459 in the spring prior to major barriers may be critical for some, if not all, of the population, determining
460 phenology and likely survival, and so ultimately population dynamics. Further research is needed to
461 determine how habitat quality further north in the northern Guinea savannah and in the Sahel
462 constrains migration ecology in sub-Saharan Africa.

463

464 **Acknowledgements**

465 This work was supported by the British Ornithologists' Union, the Linnean Society, the A.P. Leventis
466 Foundation and Chris Goodwin. We would like to thank Malcom Burgess and employees at the A.P.
467 Leventis Ornithological Institute, especially Arin Izang and Dr. Shiiwua Manu, for their significant
468 contribution to field work. Comments by Dan Chamberlain, Javier Pérez-Tris, Simeon Lisovski and two
469 anonymous reviewers significantly improved the manuscript. This is paper number (XX – number to
470 be added in proof stage) from the AP Leventis ornithological Research Institute.

471

472 References

- 473 **Alerstam, T. & Lindström, Å.** 1990. Optimal bird migration: the relative importance of time, energy,
474 and safety. E. Gwinner (Ed.), *Bird Migration: Physiology and Ecophysiology*: 331–351. Springer Berlin
475 Heidelberg.
- 476 **Arizaga, J. & Bairlein, F.** 2011. The role of age, sex, subspecies, body size and fuel load in determining
477 the social status of a migratory passerine during the non-breeding period. *Ornis Fennica* **88**: 154.
- 478 **Baillie, S.R. & Peach, W.J.** 2008. Population limitation in Palaearctic-African migrant passerines. *Ibis*
479 **134**: 120–132.
- 480 **Barshep, Y., Ottosson, U., Waldenström, J. & Hulme, M.** 2012. Non-breeding ecology of the
481 Whinchat *Saxicola rubetra* in Nigeria. *Ornis Svecica* **22**: 25–32.
- 482 **Bates, D., Maechler, M., Bolker, B. & Walker, S.** 2014. lme4: Linear mixed-effects models using
483 Eigen and S4. R package version 3.1.1.
- 484 **Bauchinger, U. & Biebach, H.** 2006. Transition between moult and migration in a long-distance
485 migratory passerine: organ flexibility in the African wintering area. *J. Ornithol.* **147**: 266–273.
- 486 **Bayly, N.J., Atkinson, P.W. & Rumsey, S.J.R.** 2012. Fuelling for the Sahara crossing: variation in site
487 use and the onset and rate of spring mass gain by 38 Palaearctic migrants in the western Sahel. *J.*
488 *Ornithol.* **153**: 931–945.
- 489 **Biebach, H.** 1992. Flight-range estimates for small trans-Saharan migrants. *Ibis* **134**: 47–54.
- 490 **BirdLife International.** 2004. *Birds in Europe: Population Estimates, Trends and Conservation Status.*
491 Birdlife International, Cambridge.
- 492 **Blackburn, E. & Cresswell, W.** 2015a. Fine-scale habitat use during the non-breeding season suggests
493 that winter habitat does not limit breeding populations of a declining long-distance Palaearctic
494 migrant. *J. Avian Biol.* **In press.**

- 495 **Blackburn, E. & Cresswell, W.** 2015b. High winter site fidelity in a long-distance migrant: implications
496 for wintering ecology and survival estimates. *J. Ornithol.* **In press.**
- 497 **Bohning-Gaese, K. & Bauer, H.-G.** 1996. Changes in species abundance, distribution, and diversity in
498 a central European bird community. *Conserv. Biol.* **10**: 175–187.
- 499 **Brandt, M.J. & Cresswell, W.** 2009. Diurnal foraging routines in a tropical bird, the rock finch
500 *Lagonosticta sanguinodorsalis* : how important is predation risk? *J. Avian Biol.* **40**: 90–94.
- 501 **Bruderer, B. & Boldt, A.** 2008. Flight characteristics of birds. *Ibis* **143**: 178–204.
- 502 **Burnham, K.P. & Anderson, D.R.** 2002. *Model selection and multimodel inference: a practical*
503 *information-theoretic approach*, 2nd Edn. Springer, New York.
- 504 **Cooper, N.W., Murphy, M.T. & Redmond, L.J.** 2009. Age- and sex-dependent spring arrival dates of
505 Eastern Kingbirds. *J. F. Ornithol.* **80**: 35–41.
- 506 **Coppack, T. & Pulido, F.** 2009. Proximate control and adaptive potential of protandrous migration in
507 birds. *Integr. Comp. Biol.* **49**: 493–506.
- 508 **Cramp, S.** 1988. *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the*
509 *Western Palaearctic*. Vol. 5: Tyrant Flycatchers to Thrushes. Oxford: Oxford University Press.
- 510 **Cresswell, W.** 2014. Migratory connectivity of Palaearctic-African migratory birds and their responses
511 to environmental change: the serial residency hypothesis. *Ibis* **156**: 493–510.
- 512 **Delingat, J., Bairlein, F. & Hedenström, A.** 2008. Obligatory barrier crossing and adaptive fuel
513 management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe*
514 *oenanthe*). *Behav. Ecol. Sociobiol.* **62**: 1069–1078.
- 515 **Dierschke, V.** 2003. Predation hazard during migratory stopover: are light or heavy birds under risk?
516 *J. Avian Biol.* **34**: 24–29.

- 517 **Fox, A. D., King, R. & Owen, M.** 2013. Wing moult and mass change in free-living mallard *Anas*
518 *platyrhynchos*. *J. Avian Biol.* **44**: 1–8.
- 519 **Francis, C.M. & Cooke, F.** 1986. Differential timing of spring migration in wood warblers (*Parulinae*).
520 *Auk* **103**: 548–556.
- 521 **Fransson, T., Jakobsson, S., Johansson, P., Kullberg, C., Lind, J. & Vallin, A.** 2001. Magnetic cues trigger
522 extensive refuelling. *Nature* **414**: 35–36.
- 523 **Fry, C.H.** 1969. Migration, moult and weights of birds in northern Guinea savanna in Nigeria and
524 Ghana. *Ostrich* **40**: 239–263.
- 525 **Gwinner, E.** 1986. Circannual rhythms: Endogenous annual clocks in the organization of seasonal
526 processes. *Berlin and New York, Springer-Verlag*.
- 527 **Hedenström, A. & Alerstam, T.** 1997. Optimum fuel loads in migratory birds: distinguishing between
528 time and energy minimization. *J. Theor. Biol.* **189**: 227–234.
- 529 **Heldbjerg, H. & Fox, T.A.D.** 2008. Long-term population declines in Danish trans-Saharan migrant
530 birds. *Bird Study* **55**: 267–279.
- 531 **Henderson, I.G., Fuller, R.J., Conway, G.J. & Gough, S.J.** 2004. Evidence for declines in populations of
532 grassland-associated birds in marginal upland areas of Britain. *Bird Study* **51**: 12–19.
- 533 **Houston, A.I. & McNamara, J.M.** 1993. A theoretical investigation of the fat reserves and mortality
534 levels of small birds in winter. *Ornis Scand*, **24**: 205–219.
- 535 **Hulme, M.F. & Cresswell, W.** 2012. Density and behaviour of Whinchats *Saxicola rubetra* on African
536 farmland suggest that winter habitat conditions do not limit European breeding populations. *Ibis* **154**:
537 680–692.
- 538 **Jenni, L. & Winkler, R.** 2011. *Moult and ageing of European passerines*. Academic Press, London.

- 539 **Jenni-Eiermann, S., Almasi, B., Maggini, I., Salewski, V., Bruderer, B., Liechti, F., & Jenni, L.** 2011.
540 Numbers, foraging and refuelling of passerine migrants at a stopover site in the western Sahara:
541 diverse strategies to cross a desert. *J. Ornithol.* **152**: 113–128.
- 542 **Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinch, C., Spina,**
543 **F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Solvang, R. &**
544 **Stenseth, N.C.** 2006. Rapid advance of spring arrival dates in long-distance migratory
545 birds. *Science* **312**: 1959–1961.
- 546 **Klaassen, M. & Lindström, Å.** 1996. Departure fuel loads in time-minimizing migrating birds can be
547 explained by the energy costs of being heavy. *J. Theor. Biol.* **183**: 29–34.
- 548 **Kullberg, C., Fransson, T. & Jakobsson, S.** 1996. Impaired predator evasion in fat blackcaps (*Sylvia*
549 *atricapilla*). *Proc. R. Soc. Lond. B* **263**: 1671–1675.
- 550 **Lind, J., Gustin, M. & Sorace, A.** 2004. Compensatory bodily changes during moult in Tree Sparrows
551 *Passer montanus* in Italy. *Ornis Fennica* **81**: 75–83.
- 552 **Maggini, I. & Bairlein, F.** 2010. Endogenous rhythms of seasonal migratory body mass changes and
553 nocturnal restlessness in different populations of Northern Wheatear *Oenanthe oenanthe*. *J. Biol.*
554 *Rhythms* **25**: 268–276.
- 555 **Maggini, I. & Bairlein, F.** 2012. Innate sex differences in the timing of spring migration in a songbird.
556 *PLoS One* **7**: e31271.
- 557 **Marra, P.P., Hobson, K.A. & Holmes, R.T.** 1998. Linking winter and summer events in a migratory bird
558 by using stable-carbon isotopes. *Science* **282**: 1884–1886.
- 559 **Marra, P.P. & Holmes, R.T.** 2001. Consequences of dominance-mediated habitat segregation in
560 American Redstarts during the nonbreeding season. *Auk* **118**: 92–104.

- 561 **McKinnon, E.A., Fraser, K.C. & Stutchbury, B.J.** 2013. New discoveries in landbird migration using
562 geolocators, and a flight plan for the future. *Auk* **130**: 211–222.
- 563 **McNamara, J.M. & Houston, A.I.** 1990. The value of fat reserves and the tradeoff between starvation
564 and predation. *Acta biotheor.* **38**: 37–61.
- 565 **Minias, P. & Kaczmarek, K.** 2013. Population-wide body mass increment at stopover sites is an
566 unreliable indicator of refuelling rates in migrating waders. *Ibis* **155**: 102–112.
- 567 **Newton, I.** 2008. *The migration ecology of birds*. Academic Press, Oxford.
- 568 **Ockendon, N., Hewson, C.M., Johnston, A., & Atkinson, P.W.** 2012. Declines in British-breeding
569 populations of Afro-Palaeartic migrant birds are linked to bioclimatic wintering zone in Africa,
570 possibly via constraints on arrival time advancement. *Bird Study* **59**: 111–125.
- 571 **Ottosson, U., Waldenström, J., Hjort, C. & McGregor, R.** 2005. Garden Warbler *Sylvia borin* migration
572 in sub-Saharan West Africa: phenology and body mass changes. *Ibis* **147**: 750–757.
- 573 **Pilastro, A. & Spina, F.** 1997. Ecological and morphological correlates of residual fat reserves in
574 passerine migrants at their spring arrival in southern Europe. *J. of Avian Biol.* **28**: 309–318.
- 575 **Piper, W.H.** 1997. *Social dominance in birds*. V. Nolan Jr., E.D. Ketterson, & C.F. Thompson (Eds.),
576 Current Ornithology, Vol. 14. Plenum Press, New York.
- 577 **R Core Team.** 2014. R: A Language and Environment for Statistical Computing. R Foundation for
578 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from: [http://www.R-](http://www.R-project.org)
579 [project.org](http://www.R-project.org).
- 580 **Risely, A., Nightingale, J., Richardson, D.S. & Barr, I.** 2013. Wing length and age, but not tarsus or
581 mass, independently determine spring arrival at breeding territories in a long-distance migrant the
582 Common Whitethroat, *Sylvia communis*. *Bird Study* **60**: 539–546.

- 583 **Salewski, V., Herremans, M. & Liechti, F.** 2010. Migrating passerines can lose more body mass
584 reversibly than previously thought. *Ringing Migr.* **25**: 22–28.
- 585 **Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & van Bommel, F.P.J.** 2006. Long-term
586 population declines in Afro-Palaeartic migrant birds. *Biol. Conserv.* **131**: 93–105.
- 587 **Schaub, M. & Jenni, L.** 2000. Body mass of six long-distance migrant passerine species along the
588 autumn migration route. *J. für Ornithol.* **141**: 441–460.
- 589 **Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L.L., Blas, J., Tavecchia, G., Preatoni, D. & Hiraldo,**
590 **F.** 2014. Individual improvements and selective mortality shape lifelong migratory
591 performance. *Nature* **515**: 410–413.
- 592 **Smith, V.W.** 1966. Autumn and spring weights of some Palaeartic migrants in central Nigeria. *Ibis*
593 **108**: 492–512.
- 594 **Stevens, M.C., Ottosson, U., McGregor, R., Brandt, M. & Cresswell, W.** 2013. Survival rates in West
595 African savanna birds. *Ostrich* **84**: 11–25.
- 596 **Stewart, R.L.M., Francis, C.M. & Massey, C.** 2002. Age-related differential timing of spring migration
597 within sexes in passerines. *Wilson Bull.* **114**: 264–271.
- 598 **Studds, C.E. & Marra, P.P.** 2005. Non-breeding habitat occupancy and population processes: an
599 upgrade experiment with a migratory bird. *Ecology* **86**: 2380–2385.
- 600 **Studds, C.E. & Marra, P.P.** 2011. Rainfall-induced changes in food availability modify the spring
601 departure programme of a migratory bird. *Proc. R. Soc. Lond. B* **278**: 3437–3443.
- 602 **Svensson, L.** 1992. *Identification Guide to European Passerines*, 4th Edn. Marstatryck, Stockholm.
- 603 **Tøttrup, A. P., & Thorup, K.** 2008. Sex-differentiated migration patterns, protandry and phenology in
604 North European songbird populations. *J. Ornithol.* **149**: 161–167.

605 **Weber, T.P. & Houston, A.I.** 1997. Flight costs, flight range and the stopover ecology of migrating
606 birds. *J. Anim. Ecol.* **66**: 297–306.

607 **Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A. & Gwinner, E.** 2003. Slow pace of life in
608 tropical sedentary birds: a common-garden experiment on four stonechat populations from different
609 latitudes. *Proc. R. Soc. Lond. B*: **270**: 2383–2388.

610 Appendices

611 Appendix A

612 Permits

613 Note that no permits are required in Nigeria to trap, colour-ring or to place geolocators on birds.
614 Nevertheless all people in this study involved in ringing and deployment of geolocators had been
615 licenced to do this within Europe for other studies and all ethical criteria and animal handling and
616 welfare procedures used were those that would have been acceptable for an equivalent study based
617 within Europe.

618 Appendix B

619 Error in departure estimates

620 Across monitored individuals (excluding early departing birds which were visited less than four times
621 after 2nd April, because averaging over so few visits is less meaningful), the probability of resighting an
622 individual during a territory visit before departure was $81 \pm 14\%$ ($n = 68$ individuals; measured simply
623 by dividing number of detections by total number of visits for each individual). There was a 96%
624 probability of detecting an individual after only two visits and a >99% probability of detection after
625 three visits. Therefore our power of observing real departures from territory rather than non-
626 detections was high and on the scale of a few days. In effect our probability of detecting a real
627 departure was likely to be much higher, because on average approximately 5-10 minutes were spent

628 looking for each missing individual initially, and then effort was increased if a bird had not been
629 detected for two consecutive visits.

630 Errors in departure date were not accounted for during analyses due to the high consistency of
631 resighting and therefore detection probability, as outlined above. Excluding birds which departed
632 prior to 2nd April (n = 5), the maximum number of consecutive days a bird was not detected when it
633 was known to be present over the monitoring period was 1.4 ± 1.1 days after last resighting (n = 70
634 individuals). Therefore variation in error of departure date for 95% of individuals would be 0 – 2.2
635 days after a bird was detected for the last time. This variation is small (9% of total variation in
636 departure range) compared to the total duration of the departure period (24 days) and therefore
637 unlikely to affect analyses.

638 Table 1. Top 10 competing candidate models to explain departure timing from wintering territory for
 639 a) birds caught in 2014 (biometric data included; n = 57) and b) all birds (biometric data not included;
 640 n = 75). Retained parameters in the models are indicated by + signs if categorical or the parameter
 641 estimate if continuous; details are given in Table 2. Grey areas indicate where the variables were not
 642 included a priori in any model. Geo = presence of geolocator tag. Date and winter of capture are not
 643 included as they were not retained in any of the top models.

a)	Sex	Age	Site	Geo	Mass	Tarsus	Time	Wing	adj R ²	F	df	logLik	ΔAICc	Weight ω
1	+								0.18	13.5	3	-186.5	0 (379.4)	0.08
2	+		+						0.22	6.1	5	-184.2	0.2	0.07
3	+		+			1.33			0.23	5.1	6	-183.3	0.9	0.05
4	+							-0.01	0.18	7.4	4	-185.9	1.1	0.05
5	+		+					-0.01	0.22	4.9	6	-183.6	1.5	0.04
6	+	+							0.18	7.0	4	-186.2	1.7	0.03
7	+		+	+					0.21	4.8	6	-183.8	1.8	0.03
8	+			+					0.17	6.9	4	-186.3	1.9	0.03
9	+					0.57			0.17	6.8	4	-186.3	2.0	0.03
10	+		+		0.66				0.21	4.7	6	-183.9	2.0	0.03
b)														
1	+		+						0.30	11.8	5	-239.4	0 (489.8)	0.3
2	+		+	+					0.31	9.3	6	-238.6	0.6	0.2
3	+			+					0.28	15.1	4	-241.4	1.7	0.1
4	+	+	+						0.29	8.7	6	-239.4	2.3	0.1
5	+								0.26	26.8	3	-242.9	2.3	0.1
6	+	+	+	+					0.30	7.4	7	-238.5	2.9	0.1
7	+	+		+					0.27	10.2	5	-241.1	3.4	0.1
8	+	+							0.25	13.2	4	-242.9	4.5	0
9		+		+					0.08	4.2	4	-250.4	19.7	0
10		+	+	+					0.10	3.1	6	-248.5	20.5	0

644

645

646

647

648

649 Table 2. Relative importance and estimates of variables hypothesized to influence departure timing
 650 in Whinchats for a) birds caught in 2014 (n = 57) and b) all birds (n = 75) for candidate models (see
 651 Table 1) within $\Delta AICc < 4$ of the top model (number of candidate models: a, n = 27; b, n = 7). Significant
 652 variables are in bold.

	a)				b)			
	Relative Importance	Estimate	2.50%	97.50%	Importance	Estimate	2.50%	97.50%
Sex (♀)	1.00	6.18	2.62	9.75	1.00	7.23	4.31	10.16
Site 1	0.5				0.71			
2		2.8	-1.40	7.01		1.67	-0.76	5.43
3		-2.3	-6.92	2.29		-1.79	-6.80	1.78
Geolocator (none)	0.18	1.56	-2.52	5.63	0.49	1.09	-0.90	5.34
Age (1 st winter)	0.17	1.38	-2.56	5.32	0.23	0.09	-3.20	3.95
Tarsus	0.26	1.08	-1.22	3.39	–	–	–	–
Mass	0.19	0.20	-1.67	2.08	–	–	–	–
Wing	0.26	-0.01	-0.03	0.01	–	–	–	–
Time	0.04	-0.35	-0.96	0.26				

653

654

655

656

657

658

659

660

661

662

663

664 Table 3. Top 10 candidate LM models predicting Whinchat mass during a) September – December
 665 (period 1; n = 176) and b) January – March (period 2; n = 164). Parameters retained in the model are
 666 indicated by + if categorical or the parameter estimate if continuous. Details are given in Table 4.

a)	Tarsus	Wing	Sex	Age	Moult	Site	Year	Date	Time	Adj R ²	F	df	logLik	ΔAICc	Weight ω
1	0.37	0.09					+			0.21	17.1	5	-212.0	0(434.4)	0.09
2	0.38	0.09					+	-0.01		0.21	13.2	6	-211.3	0.7	0.06
3	0.37	0.07	+				+			0.21	13.2	6	-211.4	0.8	0.06
4	0.38	0.10					+		0.04	0.21	13.1	6	-211.4	0.9	0.06
5	0.37	0.09			-0.13		+			0.21	12.9	6	-211.7	1.5	0.04
6	0.39	0.10					+	-0.01	0.04	0.21	10.8	7	-210.6	1.5	0.04
7	0.38	0.08	+				+		0.04	0.21	10.8	7	-210.7	1.6	0.04
8	0.38	0.08	+				+	-0.01		0.21	10.8	7	-210.8	1.8	0.04
9	0.37	0.09		+			+			0.21	12.8	6	-212.0	2.1	0.03
10	0.37	0.07	+		-0.13		+			0.21	10.6	7	-211.0	2.3	0.03
b)															
1	0.40		+	+	0.17	+		0.03	0.07	0.44	15.1	13	-241.4	0(510.9)	0.57
2	0.41	0.00	+	+	0.18	+		0.03	0.07	0.44	13.8	14	-241.1	1.7	0.25
3	0.41		+	+	0.17	+	+	0.03	0.07	0.44	12.6	15	-241.3	4.5	0.06
4	0.42	0.00	+	+	0.17	+	+	0.03	0.07	0.44	11.8	16	-241.0	6.1	0.03
5	0.45		+	+	0.14			0.03	0.07	0.41	23.2	8	-250.4	6.6	0.02
6	0.46	0.00	+	+	0.15			0.03	0.07	0.41	20.2	9	-249.5	7.0	0.02
7	0.41		+	+	0.16	+		0.02		0.42	14.9	12	-246.5	7.8	0.01
8	0.40		+		0.15	+		0.03	0.07	0.41	14.7	12	-246.9	8.7	0.01
9	0.41		+	+		+		0.03	0.07	0.41	14.7	12	-247.2	9.2	0.01
10	0.42	0.00	+	+	0.163	+		0.02		0.41	13.6	13	-246.2	9.5	0.00

667

668

669

670

671

672

673

674 Table 4. Relative importance and coefficient estimates of variables predicting mass in Whinchats
 675 during the first half of the non-breeding season (September – December) for 24 candidate models
 676 with $\Delta AICc < 4$ (see Table 3a). Significant variables are in bold.

Variable	Importance	Estimate	95% CI	
			Lower	Upper
Tarsus	1.00	0.37	0.20	0.56
Season	1.00	0.59	0.23	0.96
Wing	0.97	0.09	0.02	0.16
Sex (♀)	0.39	-0.16	-0.43	0.11
Time	0.37	0.04	-0.03	0.12
Date	0.36	0.00	-0.02	0.00
Moult	0.25	-0.12	-0.44	0.20
Age (1 st winter)	0.19	0.02	-0.27	0.23
Site	0	0	0	0

677

678

679 Table 5. Optimal general linear model identified by AICc (Table 3) identifying variables predicting mass
 680 for 196 Whinchats caught in the second half of the non-breeding period in Nigeria. Significant variables
 681 are in bold. Full model statistics: adjusted $R^2 = 0.44$, $F_{11,184} = 15.1$, $p < 0.0001$.

Variable	Estimate	95% CI		
		Lower	Upper	
Tarsus	0.40	0.22	0.58	
Date	0.03	0.02	0.04	
Sex (♀)	-0.49	-0.75	-0.23	
Age (1st winter)	-0.41	-0.66	-0.16	
Moult	0.17	0.07	0.27	
Time	0.07	0.03	0.12	
Site				
	2	-0.41	-0.81	-0.01
	3	-0.44	-0.93	0.05
	4	-0.44	-0.85	-0.02
	5	-0.87	-1.30	-0.44
	6	-0.91	-1.69	-0.13

682

683

684

685

686 **Figure Legends:**

687 Figure 1: Map of the 6 sites used in the study (see methods for details). Departure monitoring from
688 2nd April was focussed on sites 1-3, shown numbered in bold. The CES site was located between (and
689 outwith) sites 1 and 2.

690 Figure 2: Phenology of departure from territory for Whinchats in central Nigeria; a) top graph shows
691 the cumulative percent of birds departing by a particular date – all birds had departed by the 24th
692 April. The bottom histogram shows the frequency of departure on particular dates for both male and
693 female; b) departure timing relative to the earliest departing individuals (day zero) from winter
694 territory for adult and second year Whinchats of both sexes (n = 75). Note that sample size for
695 second year males is low (n = 9). For full model statistics see Tables 1 and 2.

696 Figure 3: The relationship between mass and days from departure to show predicted average mass
697 on departure (day 0 – the vertical dotted line). The solid black line shows the predicted relationship
698 using all data (<80 days from departure, $R^2 = 0.23$, $F_{1,55} = 16.1$, $P = 0.0002$), and the dotted black line
699 using <60 days from departure only ($R^2 = 0.04$, $F_{1,44} = 3.0$, $P = 0.09$). The dotted grey lines show the
700 predicted relationship using all data plus and minus two standard errors to demonstrate that all
701 relationships fitted were statistically similar. Black-filled circles represent males and grey circles
702 females.

703 Figure 4: Mass of 377 Whinchats captured over three non-breeding seasons in relation to date
704 captured (intensive study data) for the period September to March inclusive, and mass of 141
705 Whinchats captured over 8 years during April (CES ringing data): note different scales on all graphs.
706 Predicted lines are plotted for males (light grey) and females (black) from the models predicting
707 mass from date, winter season, time of day, wing length, minimum tarsus length, sex, age and
708 location, except for CES data where age and minimum tarsus data were not available. All predicted
709 lines are for an average sized bird, from the same ringing location, at 07:00, in 2013.

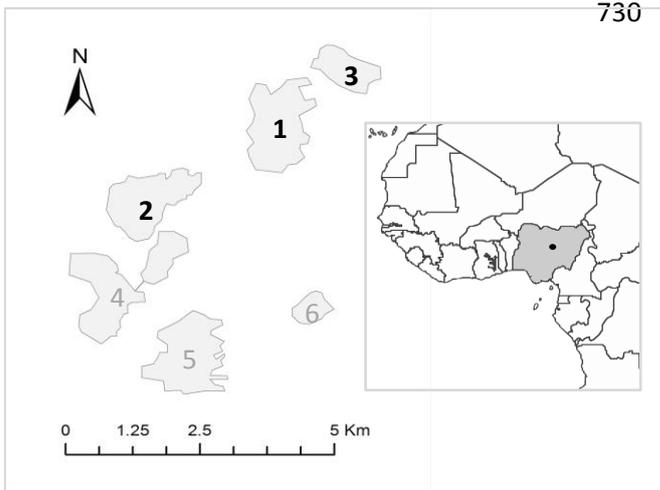
710 Figure 5: Estimated flight ranges of all Whinchats caught during April at Jos, the study site, and
711 shown by a grey dot, with a map of West Africa (shaded area is the extent of the Sahara desert)
712 scaled to the y axis and positioned with respect to the study site in the background. The grey 2,500
713 km dashed line shows the approximate shortest distance to cross the Sahara from Jos; the grey
714 2,800 dotted line the approximate distance to cross the Sahara to most northern part of Africa. The
715 heavy solid increasing curve is the cumulative percent of birds with a respective flight range
716 assuming a lean mass of 12.8 g – for example, all birds could migrate c. 400 km but only c. 5% could
717 cross the shortest part of the Sahara if they left from the study site at Jos (i.e. the intersection of the
718 dashed grey 2,500 km line with the 5% line). The dashed solid increasing curve is the cumulative
719 percent of birds with a respective flight range assuming a minimum lean mass of 11.6 g – for
720 example, all birds could migrate c. 600 km, c. 20% could cross the shortest part of the Sahara if they
721 left from the study site at Jos (i.e. the intersection of the dashed grey 2,500 km line with the 20%
722 line), and c. 5% could cross to the most northerly shore of Africa (i.e. the intersection of the dotted
723 grey line with the 5% line). (A) & (B) show two potential flight ranges estimated from the observed
724 average departure mass for resident birds, solid arrows (A) use an estimated lean mass of 12.8 g and
725 dashed arrows (B) a lean mass of 11.6 g.

726

727

728 Figure 1.

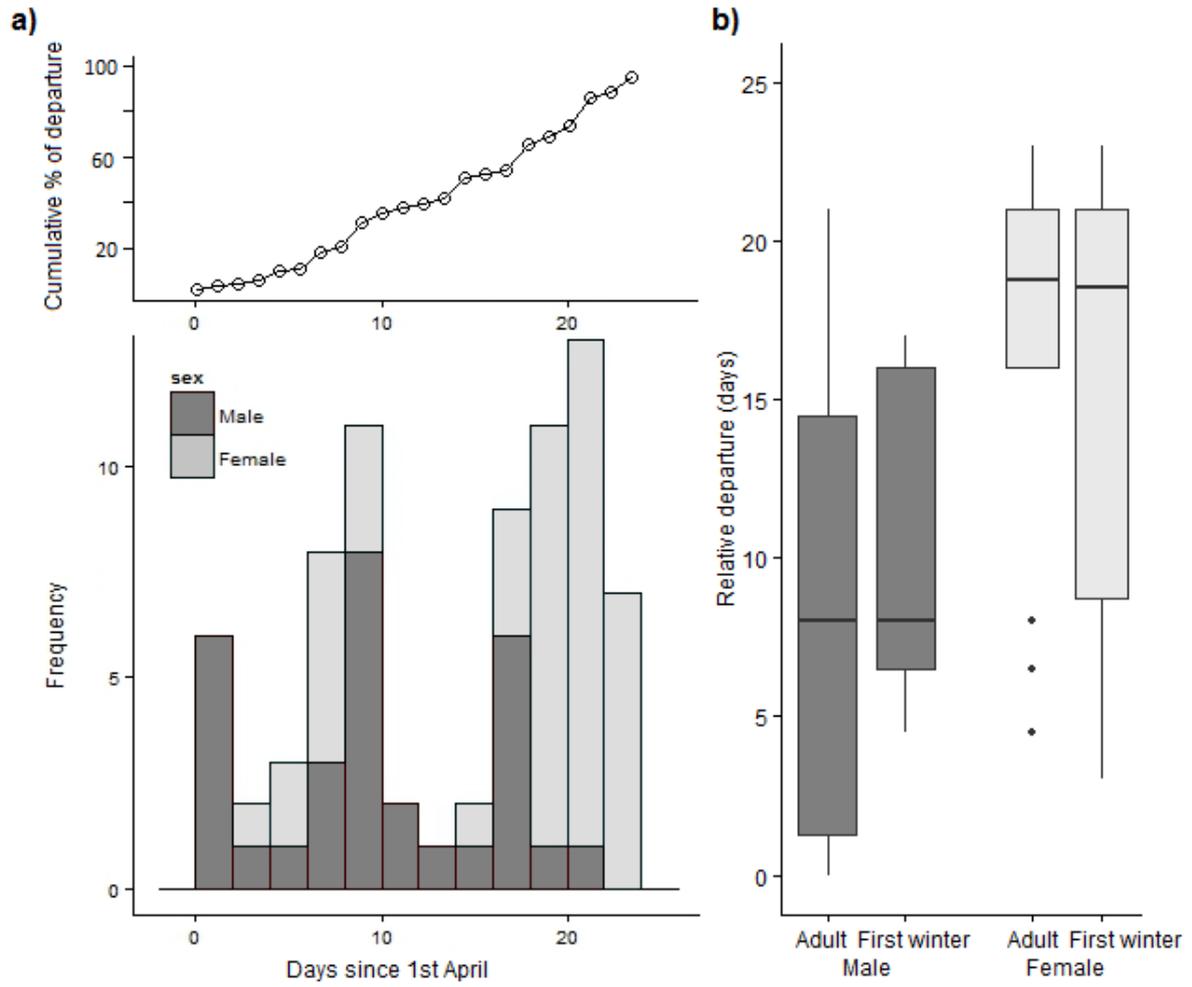
729



731 Figure 2.

732

733



734

735

736

737

738

739

740

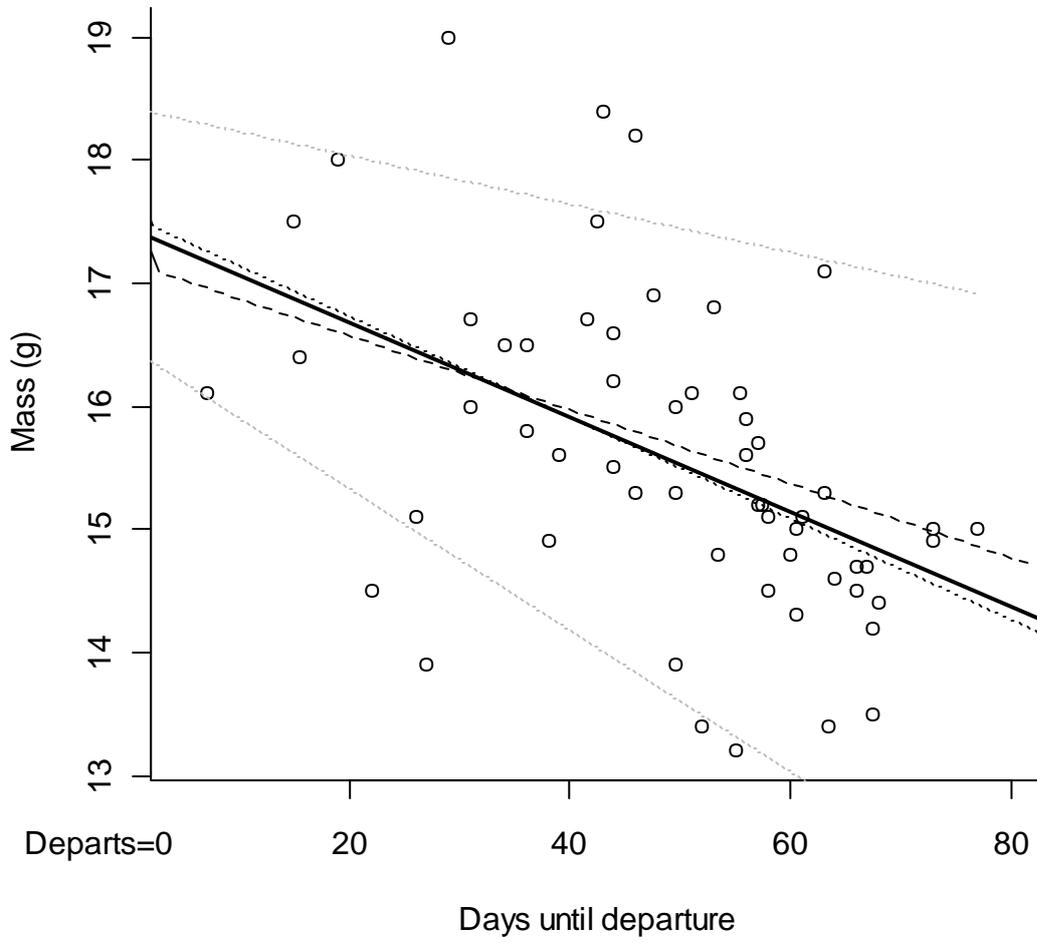
741

742

743

744

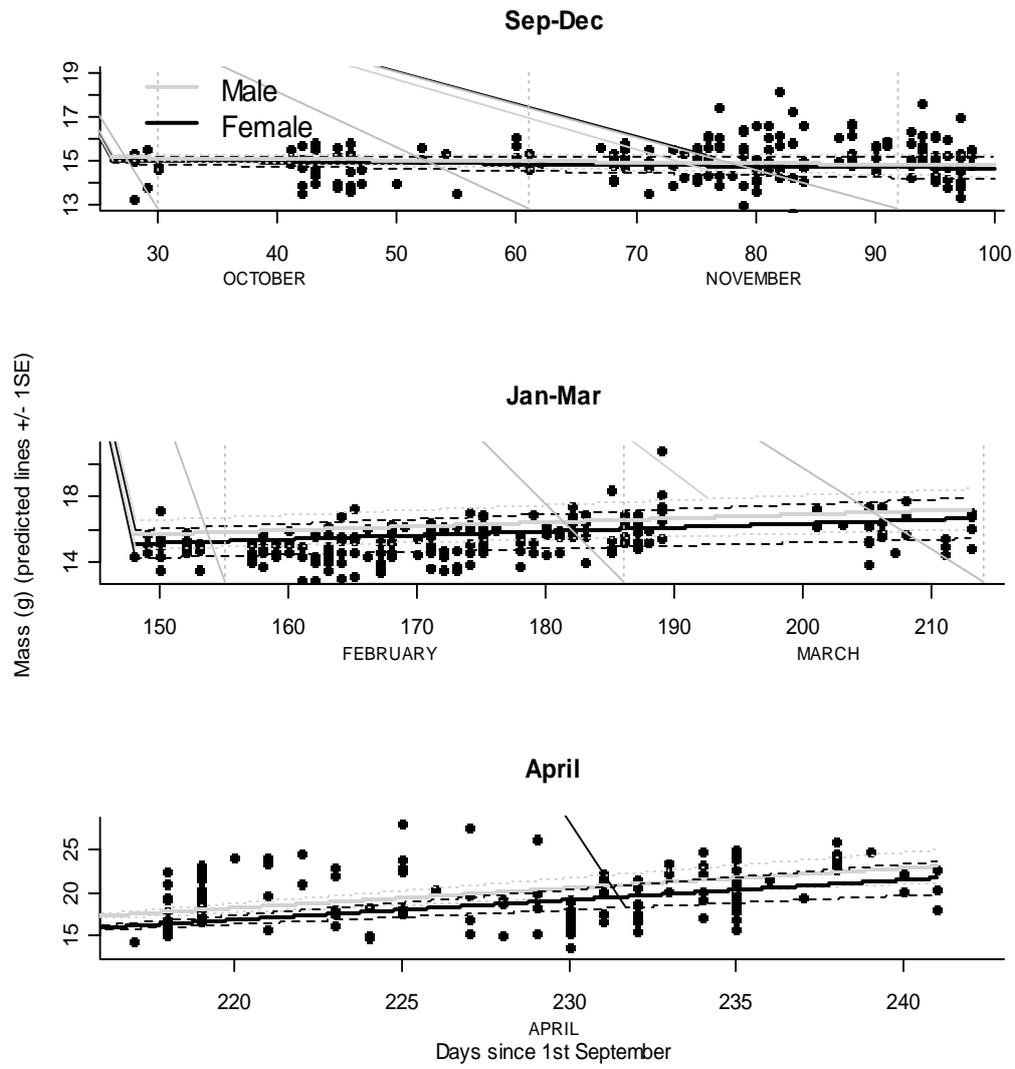
745 Figure 3.



746

747

748 Figure 4.



749

750

751

752 Figure 5.

753

